REVISIONARY STUDIES IN THE ERIOCAULACEAE OF VENEZUELA[1]

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ABSTRACT

Preparation of the Eriocaulaceae treatment for Julian Steyermark's *Flora of the Venezuelan Guayana* has brought to light a new achene-bearing subgenus, *Paepalanthus* subg. *Monosperma*, as well as the following six new species and one variety: *Eriocaulon spongiola*, *Paepalanthus chimantensis*, *P. fasciculoides*, *Syngonanthus acephalus*, *S. duidae* var. *humilis*, *S. fenestratus*, and *S. setifolius*. In addition, 14 new names or combinations are made, and some instances of synonymy are discussed.

The Guayana Highland, particularly in Venezuela, is one of the two major centers of distribution for the Eriocaulaceae in the New World, the second area being the Brazilian Central Plateau. Of the approximately 100 species of Eriocaulaceae occurring in Venezuela, about 85 occur in Guayana, 38 of which are endemic there. In preparation of the Eriocaulaceae treatment for the *Flora of the Venezuelan Guayana* (Julian Steyermark, editor), several new taxa of the region have come to light, and many revisionary changes have been found necessary. Of special interest are: *Eriocaulon spongiola*, a species with floating ribbonlike peduncles and spongy hygroscopic involucral bracts; a dimerous species of *Syngonanthus*, with exceptionally reduced inflorescences lacking peduncles and involucres; and a new subgenus of *Paepalanthus* producing single-seeded indehiscent fruits, the only known departure in the family from 3-locular capsules.

ERIOCAULON

Eriocaulon spongiola Hensold, sp. nov. TYPE: Colombia. Vaupés: Rio Apaporis, Rio Piraparaná, Cano Teemeeña, between 0°15′S, 70°30′W and 0°25′N, 70°30′W, *Schultes & Cabrera 17314* (holotype, US; isotype, MO). Figures 1, 2.

Planta aquatica caulescens. Folia fasciaria, membranacea, valde fenestrata, fluitantia, usque 30 cm longa et 5–7 mm lata. Pedunculi basin versus filiformes apicem versus fasciarii, fenestrati, 2–3 mm lati, folia simulantes. Capitula 5–6 mm lata. Bracteae involucrales pallide brunneae, apicibus spongiosis hygroscopicis auctae. Flores trimeri; sepala libera vel in spatha connata; petala subaequalia; antherae albidae.

Plants aquatics in shallow streams, the base rooted, the stems, leaves, and peduncles submerged or floating. Roots relatively fine, ca. 0.5 mm diam. Stems up to 25–30 cm long, ca. 1–2.5 mm wide, glabrous. Leaves linear, ribbonlike, up to 30 cm or longer and 5–7 mm wide, membranous, glabrous, the tips often broken off, conspicuously fenestrate from base to apex, the longitudinal and transverse striations of about equal thickness. Inflorescence arrangement unknown (peduncles not attached to the stem in the available material). Peduncles 40–50 cm long, filiform at base, broadening and ribbonlike toward the apex, up to 2.5–4 mm wide, membranous, glabrous, fenestrate like the leaves, not evidently costate. Capitula 5–6 mm diam., hemispheric to ovoid, with an elongate receptacle. Involucral bracts in only 1–2 series, orbicular or somewhat tapered toward the irregularly rounded apex, ca. 1.5–2.2 mm long and nearly as wide, spongy, pale brownish, glabrous. Floral bracts similar in size and color to the involucral bracts, the base broad, carinate, and membranous, held perpendicular to the elongate receptacle and cupping the flowers, the apex abruptly differentiated from the base, broadly rounded to truncate or

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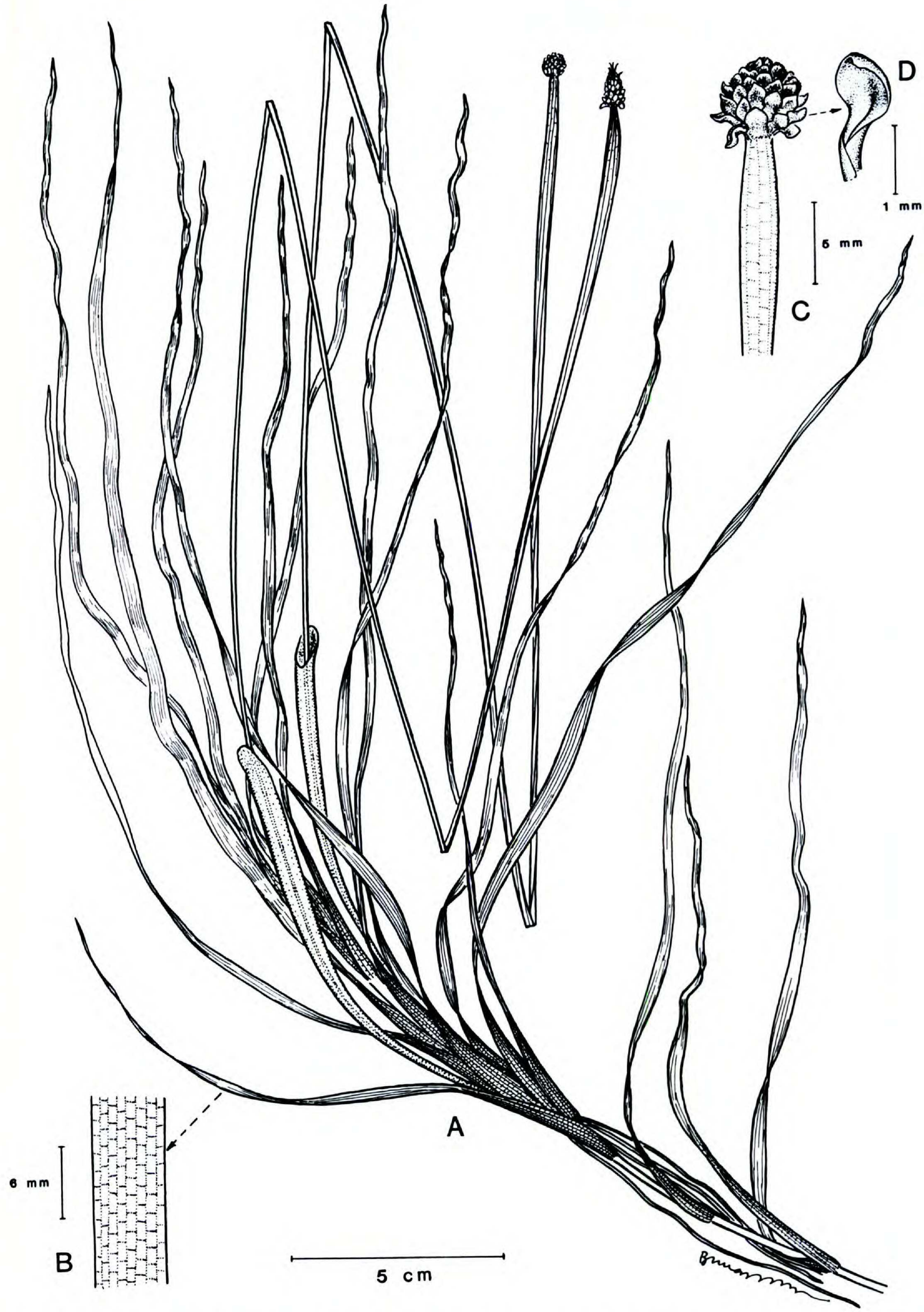

FIGURE 1. *Eriocaulon spongiola* Hensold (*Schultes & Cabrera 17314* US).—A. Habit.—B. Leaf.—C. Inflorescence.—D. Involucral bract.

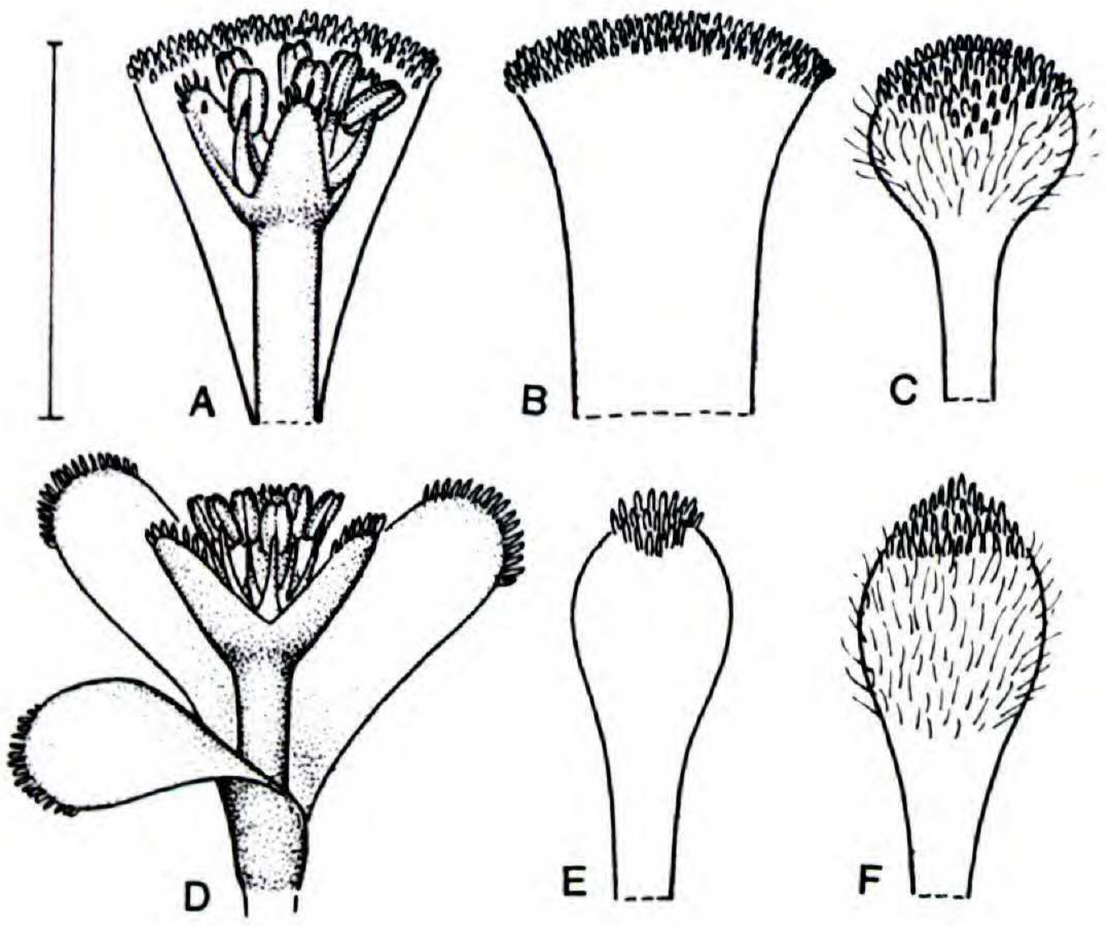

FIGURE 2. *Eriocaulon spongiola* Hensold. A–C. *Berry 746* (VEN).—A. Staminate flower, the calyx fused into a truncate spathe. B, C. Pistillate flower.—B. Calyx.—C. Petal, adaxial view. D, E. *Schultes & Cabrera 17314* (US).—D. Staminate flower, the calyx only shallowly fused, regular. E, F. Pistillate flower.—E. Sepal, abaxial view.—F. Petal, adaxial view. Scale bar = 1.5 mm.

triangular-obtuse (progressively smaller distally), spongy, hygroscopic, expanding and folding upward against the surface of the capitulum to enclose the flowers when wet, pilose abaxially with white, clavate hairs in a transverse band below the apex. *Staminate flowers*. Sepals 3, free, oblong and rounded (Colombia) or completely fused into a cuneate, perfectly truncate adaxial spathe (Venezuela), in either case ca. 1.9–2.4 mm long, light brown, membranous, densely ciliate with white clavate hairs at the upper margin. Androphore ca. 1.3–2.0 mm long, ca. 0.25 mm diam. Petals free, equal or subequal, ca. 0.4 mm long, pilose at the upper margin and adaxially at the apex, glandular (Venezuela) or not (Colombia). Stamens with filaments about equaling the petals; anthers white, ca. 0.25 mm long. *Pistillate flowers*. Sepals 3, free, spatulate (Colombia) or completely fused into a spathe as in the staminate flowers (Venezuela), in either case ca. 1.5–1.6 mm long, the same color, texture, and pubescence as in the staminate flowers. Petals free, broadly spatulate, rounded, about equaling the sepals, tufted with white clavate hairs adaxially at apex, and also pubescent with curly brownish filamentous hairs adaxially below apex, glandular (Venezuela) or not (Colombia).

Additional specimen examined. VENEZUELA. AMAZONAS: in caño ca. 4 km S of Macuruco on road to Santa Bárbara del Orinoco, *Berry 746* (VEN) (inflorescences only).

This species had previously been mistaken for *E. spruceanum* Koern., which also may have floating, membranous, ribbonlike leaves, and which may occur in the same general area (though it is not known from Venezuelan Guayana). *Eriocaulon spongiola* is easily distinguished by its elongate stem, its very conspicuously fenestrate leaves, and particularly by its fenestrate, membranous peduncles and the spongy, hygroscopic apices of the floral bracts. *Eriocaulon spruceanum* also has fenestrate leaves, but these often must be held up to the light for the transverse striations to be clearly seen, and these tend to be finer and less conspicuous than the longitudinal striations. In addition, *E. spruceanum* almost always has firm, erect, conspicuously costate peduncles, which are never fenestrate.

Because floral morphology, particularly sepal form and fusion, seems to be a very plastic character in *Eriocaulon*, I have not recognized the Venezuelan material, with sepals fused into a cuneate spathe, as distinct from the Colombian material, with the sepals completely free.

PAEPALANTHUS

Paepalanthus subg. **Monosperma** Hensold, subg. nov. TYPE: *Paepalanthus squamuliferus* (Mold.)

Herba perennis caulescens vel rosulata rhizomatosa. Radices veteres saepe villosae. Flores pistillati: Sepala demum non nisi secus costam incrassata, in capitulo remanentia. Petala plerumque dense longiciliata, demum omnino incrassata cum fructu dispersa. Appendices styli plerumque nigricantes, non nisi apice papillosae, ramulos styli fere aequantes. Stigmata bifida. Ovarium semen unum efferens; fructus achenium.

Caulescent or rhizomatous rosulate perennial herbs. Roots firm, usually whitish, the epidermis even of older roots, often persistently villous on exposed aboveground portions. Leaves linear to ligulate or lanceolate, chartaceous to coriaceous, smooth above and striate below or the upper surface 1–3-sulcate, variously pubescent with filamentous hairs. Inflorescences solitary to numerous, the peduncle sheaths foliaceous with an acute apex. Capitula 4–16 mm diam., hemispheric to globose or fungiform. Involucral bracts mostly dark blackish brown, occasionally paler and then dull yellow-brown or copper-colored, ± ovate, the apex obtuse to acute, acuminate or apiculate, enclosing but never surpassing the head, glabrous to ciliate and abaxially sericeous. Receptacle pilose. Floral bracts oblanceolate to oblong or squarish, subequaling the flowers, dark brown, barbate abaxially at apex, the

trichomes linear-obtuse to clavate, granular within. Flowers 3-merous, unisexual, actinomorphic, short-pedicellate. *Staminate flowers*. Sepals free or briefly connate at base, oblanceolate to obovate, acute to rounded, dark brown, barbate abaxially. Corolla tubular, borne on an androphore, the androphore commonly stout and about equal to corolla tube in length, though sometimes much shorter, the tube rather narrowly infundibular, membranous, the lobes 3 and sharply triangular-acute or sometimes low, rounded, and irregular. Filaments free, the anthers exsert, white to brown. Pistillodes large, simulating appendages of gynoecium. *Pistillate flowers*. Sepals free, obovate to sometimes ovate or oblong, similar in color and pubescence to those of staminate flowers, the midrib area thickened and pale in fruit. Petals oblong to narrowly elliptic, lanceolate or oblanceolate, usually much narrower than sepals, blackish streaked, and usually densely pubescent with very long cilia, especially toward the base, rarely (*P. chimantensis*) subglabrous, thickening throughout and the tips recurving at maturity, dispersed with the fruit. Staminodes present at base of petals, small and scalelike and appressed against the ovary. Ovary dark blackish brown, producing a single seed, the two abortive locules represented by ridges in fruit; style frequently equaling or exceeding the style branches in length, never less than ½ the length of the style branches, robust, often somewhat swollen above, easily breaking just above the ovary, not dispersed with fruit; appendages large, stalked, fusiform to clavate, with the main body smooth and usually blackish, white-papillate only at the upper rim, about ⅔ to equal the length of the style branches; style branches shallowly bifid. Fruit an indehiscent single-seeded asymmetrically fusiform achene.

This subgenus comprises 23 species, all of which are endemic to the Guayana Shield of Venezuela, Amazonian Brazil, and Guyana. Most of the species are narrow endemics to the summits of one or few tepui formations. They are closely related to each other, distinguished by subtle, reticulately varying characters, and show some evidence of hybridization. This variation pattern is similar to that seen in certain eriocaul taxa of the Brazilian highlands (e.g., *Paepalanthus* subg. *Xeractis* and *Aphorocaulon*, and *Syngonanthus* sect. *Eulepis* in the Serra do Espinhaço of Minas Gerais). Although the topography of the Brazilian and Venezuelan highlands is very different, both areas represent seasonally wet high-altitude formations with thin, nutrient-poor soils.

Paepalanthus subg. *Monosperma* is the only subgenus of *Paepalanthus* to have undergone radiation on the tepui summits of Venezuela. Members of a few other alliances occasionally reach tepui summits (*P. dichotomus* Klotzsch ex Koern., *P. tortilis* (Bong.) Koern., and *P. formosus* Mold.), but the main distribution of these species and their allies is elsewhere.

This subgenus is best characterized by the apparently consistent production of single-seeded indehiscent fruits, in contrast to the capsular fruits produced by all other taxa known in the family. The achenes are dark-colored and thin-walled, not differing greatly in appearance from fruits of other *Paepalanthus* in which by chance only a single ovule has matured. At anthesis, the ovaries of subg. *Monosperma* are to my eye indistinguishable from those of other subgenera. It remains to be shown whether only one functional ovule is produced, or whether all three ovules are functional, with the development of more than one seed chemically inhibited. Thomas Stützel (pers. comm.) has pointed out that a consistent position of the fertile locule would provide evidence for the first possibility. Unfortunately, because the position of the "fertile locule" cannot be readily distinguished before seed set, and seed set occurs concomitant with abscission of floral parts from the axis, I have not been able to answer this question with the material at hand.

Whatever the mechanism, the character of single seed production appears to be constant throughout the subgenus. The regular abscission of the style from the apex of the ovary is further evidence that the character is genetically fixed. Such abscission is not observed in the capsular-fruited species, in which the seed, not the fruit, is the dispersal unit. Similarly, the sclerification of the petal bases in fruit also may be interpreted as evolutionarily correlated with indehiscent fruit production, because in capsular fruits this sclerification would impede seed dispersal.

Characters other than fruit type useful in distinguishing the subgenus are: (1) the villous indumentum on exposed portions of the root; (2) the sclerification of both perianth whorls of the pistillate flower in fruit (and not merely the sepals); (3) the relative weakness of sclerification of the sepals of pistillate flowers, and their failure to recoil hygroscopically upon drying, being left behind in the capitulum after fruit dispersal; (4) the extreme hairiness of the petals of the pistillate flowers in all but one species (*P. chimantensis*); (5) the very fleshy elongate style with long darkly pigmented nectaries papillate only at the upper rim (see flower of *P. chimantensis*, Fig. 4); and (6) the regular abscission of the style at fruiting.

It is not possible at this time to make a rigorous

comparison with other subgenera because the genus as a whole is poorly known, especially with respect to floral characters. The most complete description possible is provided in order to facilitate future comparisons with other as yet poorly known groups. Characters 1, 2, 5, and 6, above are to my knowledge rather exceptional in the genus. Characters 3 and 4 are useful in identification but are also found in other taxa.

The affinities of this subgenus are not yet clear, though it bears some similarity to a complex of capsular-fruited species native to the West Indies, represented by *Paepalanthus seslerioides* Griseb. and *P. retusus* Wright.

A list of accepted taxa and synonyms to be placed in the subgenus follows.

1. *P. apacarensis* Mold.
2. *P. auyantepuiensis* Mold.
3. *P. cardonae* Mold.
4. *P. chimantensis* Hensold, sp. nov.
5. *P. convexus* Gleason
6. *P. cumbricola* Mold.
7. *P. fraternus* N. E. Br.
8. *P. fulgidus* Mold.
   P. perplexans var. *steyermarkii* Mold. (syn.)
9. *P. gleasonii* Mold.
   P. robustus Gleason (syn.)
   P. convexus var. *strigosus* Mold. (syn.)
10. *P. holstii* Steyerm.
11. *P. kunhardtii* Mold.
12. *P. major* (Mold.) Hensold, comb. nov. (see below)
13. *P. parvicephalus* (Mold.) Hensold, comb. et stat. nov. (see below)

13a. *P. parvicephalus* var. *parvicephalus*

13b. *P. parvicephalus* var. *wurdackii* (Mold.) Hensold, comb. nov. (see below)

14. *P. phelpsae* Mold.
15. *P. roraimensis* Mold.
    Rondonanthus micropetalus Mold. (syn.)
16. *P. schomburgkii* Klotzsch ex Koern.
    P. perplexans Mold. (syn.)
    P. pendulus Mold. (syn.)
    P. macrocaulon var. *venamensis* Mold. (syn.)
17. *P. scopulorum* Mold.
    P. scopulorum var. *auyantepuiensis* Mold. (syn.)
18. *P. squamuliferus* Mold.
    P. fraternus var. *spathulatus* Mold. (syn.)
19. *P. stegolepoides* Mold.
    P. fraternus var. *chimantensis* Mold. (syn.)
20. *P. subcaulescens* N. E. Br.
21. *P. sulcatus* Hensold
    P. stegolepoides var. *acutalis* Mold. (syn.)
22. *P. turbinatus* (Gleason) Hensold, comb. nov. (see below)
23. *P. venustus* Mold.
    P. venustoides Mold. (syn.)

Paepalanthus chimantensis Hensold, sp. nov.

TYPE: Venezuela. Bolívar: Apácara-tepui, Chimantá Massif, 2,200 m, 30 Jan.–1 Feb. 1983, *Huber & Steyermark 6971* (holotype, MO; isotype, VEN). Figures 3F, G, 4.

Herba perennis rosulata. Folia 3–4.5 cm longa, 3–8 mm lata, valde mucronata, subtus striata superne laevia nitida ubique glabra. Pedunculi ca. 13–30 cm longi basin versus glabri ad apicem sericeo-tomentosi. Capitula 6.5–9 mm lata. Bracteae involucrales griseo-brunneae angusteovatae plerumque breviter acuminatae, proximales distales subaequantes. Fructus achenium.

Rosulate rhizomatous perennials forming small clumps. Roots pale, fibrous. Leaves chartaceous, glabrous, often bluish green, 3–4.5 cm long, 3–8 mm wide at middle, tapered, usually rounded toward the apex, distinctly mucronate, the upper surface lustrous, especially shiny toward the margins, the lower surface striate. Inflorescences 1–6 per cohort, synchronous; peduncle sheaths equaling to exceeding leaves by up to 3.0 cm, glabrous, the apex acute to acuminate; peduncles ca. 13–30 cm long, 4–5-costate, lightly tomentose at least when young with mixed retrorse and antrorse hairs, usually glabrate toward base and more densely and persistently sericeo-tomentose distally. Heads 6.5–9 mm diam., hemispheric to subglobose at maturity; involucral bracts gray-brown, lustrous, ciliate in bud but early glabrate, lance-ovate, usually aristate or short-acuminate, the lower bracts slightly narrower than but usually as long as the upper, and usually with a slightly thickened reddish midrib. Floral bracts about equaling the flowers, obovate to linear-subspatulate, fuscous, subhyaline, ciliate at upper margin and tufted along midvein abaxially with opaque white clavate hairs. *Staminate flowers.* Pedicels ca. 1.0 mm long. Sepals 3, free, elliptic to narrowly obovate, acute, ca. 1.9–2.5 mm long, 0.7–1.2 mm wide, fuscous, pubescent as floral bracts; corolla tube borne on an androphore ca. 0.5–0.75 mm long, the tube itself 1.0–1.5 mm long, narrowly infundibular, the lobes 3, narrowly triangular, acute; anthers cream to brownish, strongly exsert; pistillodes 3, simulating gynoecial appendages and nearly the length of the tube. *Pistillate flowers.* Sepals 3, free, broadly obovate-elliptic, acute, carinate, ca. 2.8 mm long, 1.6 mm wide, fuscous at least toward the apex, pubescent as in the staminate flowers, the midvein area thickening and expanding at maturity toward

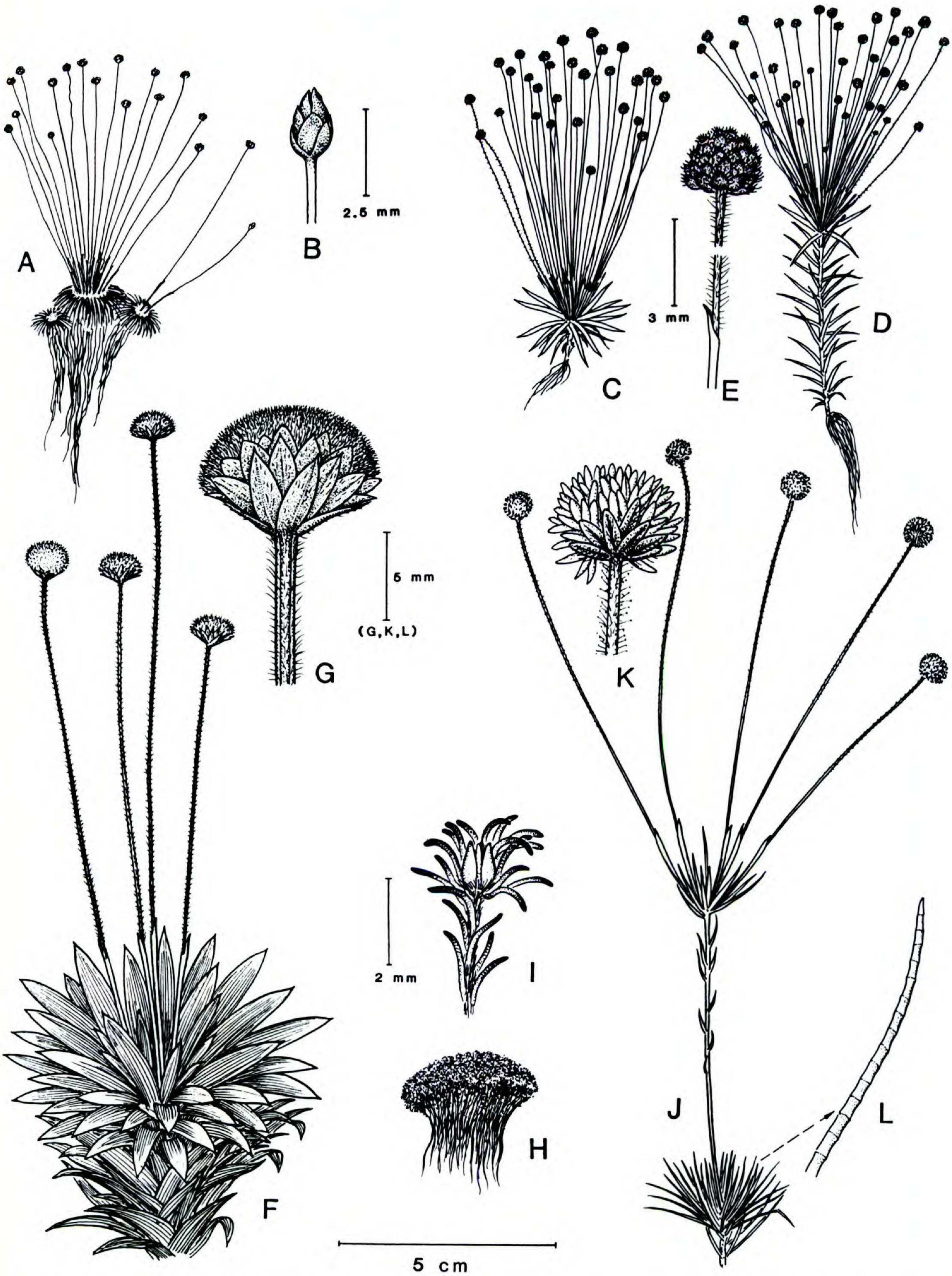

FIGURE 3. Habits of *Syngonanthus setifolius* Hensold, *Paepalanthus fasciculoides* Hensold, *P. chimantensis* Hensold, *S. acephalus* Hensold, and *S. fenestratus* Hensold. A, B. *S. setifolius* (*Liesner 3914* MO).—A. Habit.—B. Inflorescence in bud. C–E. *P. fasciculoides* (*Silva et al. 1756* MO).—C, D. Habit.—E. Inflorescence. F, G. *P. chimantensis* (*Huber 11598* MO).—F. Habit.—G. Inflorescence. H, I. *S. acephalus* (*Vareschi & Magdefrau 6789* VEN).—H. Habit.—I. Fertile branch with terminal flower. J–L. *S. fenestratus* (*Vareschi & Magdefrau 6612* VEN).—J. Habit.—K. Inflorescence.—L. Leaf. Scale bar at base applies to all habit illustrations.

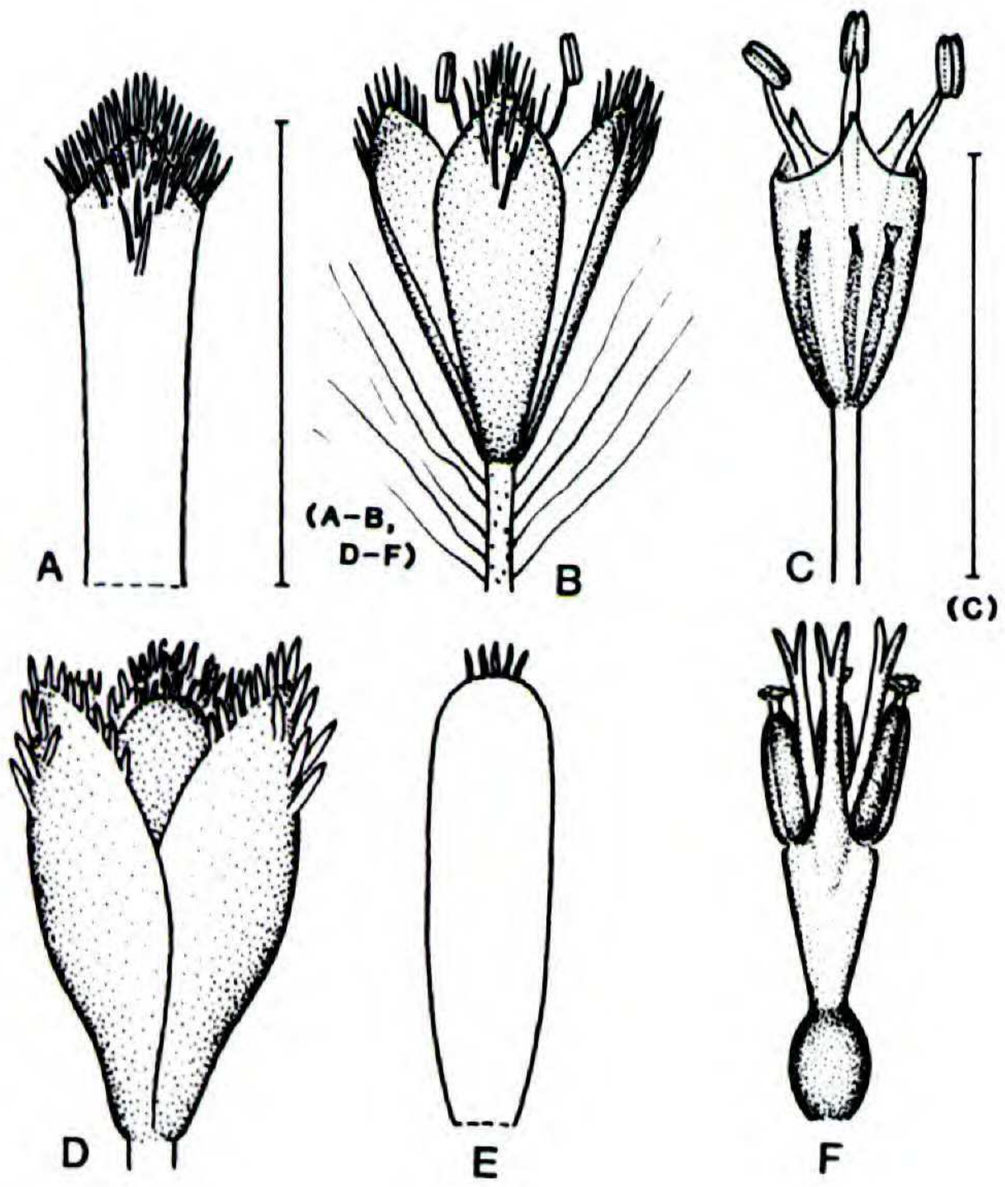

FIGURE 4. *Paepalanthus chimantensis* Hensold (*Huber & Steyermark 6971* MO). A–C. Staminate flower.—A. Floral bract.—B. Flower.—C. Flower with sepals removed. D–F. Pistillate flower.—D. Flower.—E. Petal.—F. Gynoecium. Scale bar A–B, D–F = 3 mm; scale bar C = 2 mm.

the base, sepals remaining after dispersal of fruit; petals oblong to elliptic, rounded at apex, ca. 2.7 mm long, 0.8 mm wide, glabrous or sparingly ciliate along upper margins, expanding and thickening at maturity and dispersed with the fruit. Ovary ca. 0.75 mm long, blackish, with one functional locule, the style 0.9 mm long, 3-angled and expanded above, broadest just below divergence of the appendages, where it about equals the ovary in diameter; appendages 3, ca. 0.9 mm long, fusiform-terete, smooth and blackish except for the pale papillate apex; style branches diverging slightly but distinctly above the appendages, ca. 1.0 mm long, shallowly bifid, slightly exsert. Fruit an achene.

Additional specimens examined. VENEZUELA. BOLÍVAR: Chimantá Massif, Apácara-tepui, 2,100–2,200 m, *Huber & Steyermark 7035* (VEN), *Huber et al. 8817* (NY), *Huber et al. 8823* (NY), *Steyermark 128376* (LL, MO); Chimantá Massif, C. section, 2,120 m, *Steyermark & Wurdack 750* (F, NY), *Steyermark & Wurdack 764* (F, NY); Chimantá Massif, Murey- (Eruoda-) tepui, 2,600 m, *Huber 11598* (MO).

This distinctive Chimantá Massif endemic is a member of subg. *Monosperma*. It has previously been confused with *Paepalanthus kunhardtii* Mold., *P. schomburgkii* Klotzsch ex Koern., and *Leiothrix turbinata* Gleason (see *P. turbinatus* below). It is best distinguished by its rosulate habit, glossy glabrous sharp-mucronate leaves, more or less oblong grayish involucral bracts, and the petals of the pistillate flowers which equal the sepals and are subglabrous. It has been collected in flower from January to March.

This species is unrelated to the unpublished herbarium name "Paepalanthus chimantensis," which Moldenke (1957) mentions as a synonym of *Carptotepala jenmanii* (Gleason) Mold.

Paepalanthus dichotomus Klotzsch ex Koern. in C. Martius, Fl. Bras. 3(1): 348. 1863. *Dupatya dichotoma* (Klotzsch ex Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. TYPE: Venezuela. Bolívar: Rué-imeru falls, *Schomburgk 899* (holotype, B not seen; F photo neg. #10597).

Paepalanthus guyanensis Klotzsch ex Koern. in C. Martius, Fl. Bras. 3(1): 347. 1863. *Dupatya guyanensis* (Klotzsch ex Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. TYPE: Venezuela. Bolívar: Rué-imeru falls, *Schomburgk s.n.* (holotype, B not seen). Syn. nov.

Syngonanthus savannarum Mold., Bull. Torrey Bot. Club 75: 202. 1948. *Paepalanthus savannarum* (Mold.) Mold., Phytologia 49: 293. 1981. TYPE: Guyana. Kaieteur Savanna, *Maguire & Fanshawe 23280* (holotype, NY; isotypes, F, MO). Syn. nov.

Paepalanthus steyermarkii Mold., Fieldiana, Bot. 28: 125. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, between Kavanayén and Río Karuai, 1,220 m, *Steyermark 59369* (holotype, NY; isotype, MO). Syn. nov.

Syngonanthus venezuelensis Mold., Fieldiana, Bot. 28: 128. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, between Kavanayén and Río Karuai, 1,220 m, *Steyermark 59347* (holotype, NY; isotypes, F, MO). Syn. nov.

Syngonanthus savannarum var. *glabrescens* Mold., Mem. New York Bot. Gard. 9: 412. 1957. *Paepalanthus savannarum* var. *glabrescens* (Mold.) Mold., Phytologia 49: 293. 1981. TYPE: Venezuela. Bolívar: Chimantá Massif, C. section, base of upper falls of Rio Tírica, *Steyermark & Wurdack 539* (holotype, NY; isotype, F). Syn. nov.

Paepalanthus apacarensis var. *humilis* Mold., Phytologia 54: 66. 1983. TYPE: Venezuela. Bolívar: Chimantá Massif, central NE sector of Chimantá-tepui, E headwaters of Caño Chimantá, *Steyermark 128164* (holotype, LL not seen). Syn. nov.

Paepalanthus dichotomus, endemic to the Gran Sabana of Venezuela and adjacent Guyana, has previously been recognized under several names, probably owing to the large variation found in pubescence, leaf texture, and peduncle elongation. However, these characters are found to vary continuously and independently of each other, and the segregation of distinct taxa within this complex is not supportable. That some of the taxa were de-

scribed in *Syngonanthus* probably owes to the tight coherence of the apices of the pistillate flower petals, which are nonetheless not truly fused. In other respects (fibrous roots, sepals tufted with trichomes, trichomes often tuberculate with ornamented internal walls, sepals of the pistillate flowers hygroscopic and thickening and recoiling to eject fruit at maturity), this species is definitely allied to *Paepalanthus*.

Paepalanthus fasciculoides Hensold, sp. nov.
TYPE: Brazil. Pará: Marabá, Serra dos Carajás, 700–750 m, *A. S. L. da Silva et al. 1756* (holotype, MO; isotype, NY). Figures 3C–E, 5.

Herba annua erecta caulescens. Folia linearia ca. 5–10 mm longa, 0.5–1 mm lata attenuata, superne hispida. Inflorescentiae multae terminaliter fasciculatae. Capitula ca. 2 mm lata, globosa. Bracteae involucrales fuscae late oblongo-obovatae, ciliatae; bracteae florales eis similes, rotundatae dense ciliatae, infra apicem abaxialiter barbatae. Sepala florum staminatorum fusca oblanceolata basi attenuata.

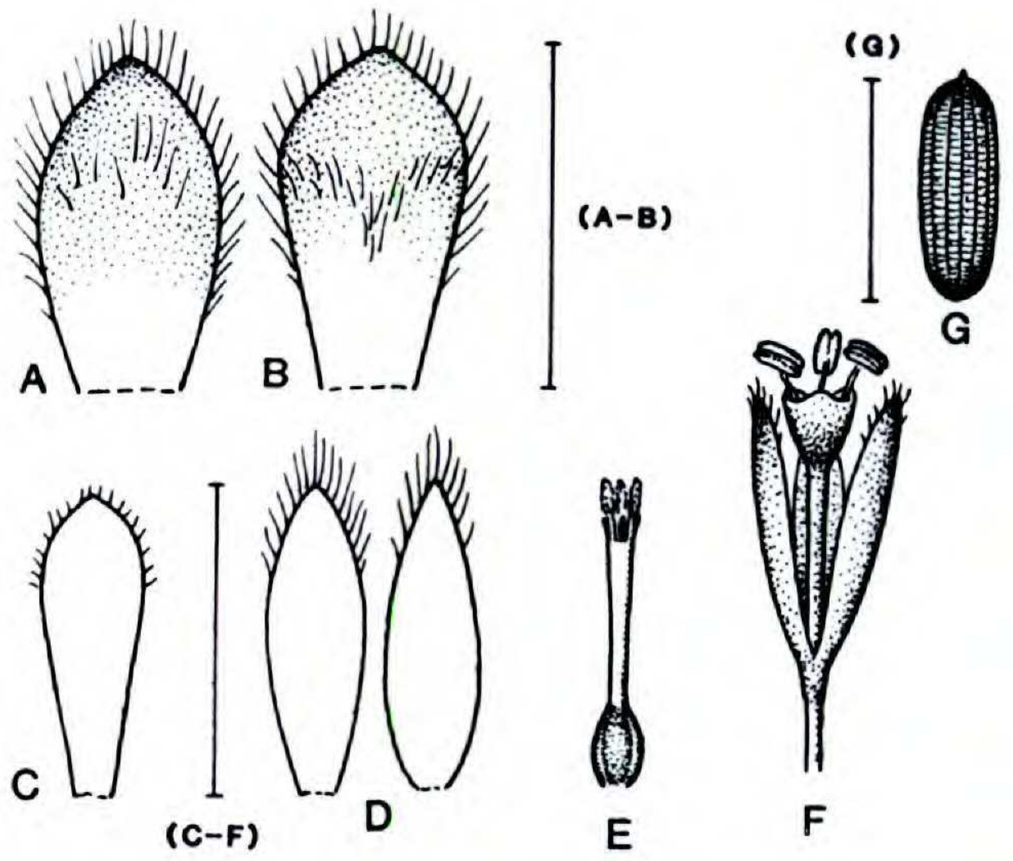

FIGURE 5. *Paepalanthus fasciculoides* Hensold (*Silva et al. 1756* MO).—A. Involucral bract.—B. Floral bract. C–E. Pistillate flower.—C. Sepal.—D. Petals.—E. Gynoecium.—F. Staminate flower.—G. Seed. Scale bar A–B = 1 mm; scale bar C–F = 1 mm; scale bar G = 0.6 mm.

Plants annuals with leafy stems up to ca. 5 cm long. Leaves dark green, ca. 5–10 mm long, 0.5–1 mm wide, longer toward stem apex, attenuate, not ampliate at base, spreading, the upper surface hispid (with short, stiff hairs). Inflorescences numerous and clustered at stem apex. Peduncle sheaths with the apex attenuate-acute and often deflexed at right angles. Peduncles ca. 2–5 cm long, pilose with long spreading hairs, green, obscurely 3-costate. Heads 2–3 mm diam., globose. Involucral bracts dark fuscous, broadly oblong-obovate, obtuse, concave to navicular, ca. 1.2–1.5 mm long, densely ciliate at upper margin and sparsely pilose in medial area on abaxial side. Floral bracts similar in size to involucral bracts, also fuscous, broadly spatulate and rounded or obtuse at apex, navicular, distinctly narrowed toward base, ciliate along upper margin and densely bearded in a V-shaped medial band below apex. *Staminate flowers*. Pedicels ca. 0.3–0.5 mm long. Sepals 3, connate at base, oblanceolate, acute, ca. 1.2 mm long, fuscous at least apically, ciliate at upper margin, enough narrowed at base so that the androphore is visible without teasing the bases apart. Corolla inserted on a very long androphore nearly equaling the sepals, the tube itself at least partially exsert from the calyx; anthers white, ca. 0.3 mm long. *Pistillate flowers*. Sepals 3, connate very briefly at base, linear-spatulate, ca. 1.0 mm long at anthesis, cream-colored, sparsely ciliate at upper margin, thickening, elongating and recoiling hygroscopically at fruiting. Petals hyaline, oblong, obtuse to acute, ciliate along the distal margin, about equaling the sepals. Gynoecium with style 2–3 times the length of the style branches; style branches simple, about twice the length of the filiform appendages. Seeds oblong, 0.6 mm long and less than half as wide, yellow-brown, the testa with prominent longitudinal striations.

Additional specimens examined. VENEZUELA. BOLÍVAR: Cerro Cotorra (El Vigía), south side of Río Paragua between La Paragua and San Pedro de Las Bocas, 600 m, 5 Aug. 1960, *Steyermark 86888* (VEN). BRAZIL. PARÁ: Marabá, Serra dos Carajás, solo com cascalho de pedras, *M.G. Silva 2920* (NY); Marabá, Serra Norte, Carajás, N1, on canga outcrop, May 1986, *Marli et al. 70* (SPF).

Paepalanthus fasciculoides is distinguished from its closest relative, *Paepalanthus fasciculatus*, by the dark brown obovate to spatulate involucral and floral bracts with entire upper margins, the dense subapical bearding of the floral bracts, and the narrow oblanceolate sepals. In *P. fasciculatus*, the bracts are buff-colored, usually conspicuously mucronate or apiculate, and at least the floral bracts are usually rather broadly obtrullate with a flattish upper margin. Instead of being densely bearded, they are generally sparsely pilose in one medial or two submedial bands. The sepals of the staminate flowers in *P. fasciculatus* are more or less broadly elliptic, the lateral margins overlapping each other and concealing the basal part of the corolla. The two species may also be ecologically distinct, the rarer *P. fasciculoides* being found only on rocky soils and canga in low mountains of Amazonian Brazil and Venezuelan Guayana, while *P. fascicu-*

latus is a common species of sand savannas at low altitudes.

Paepalanthus major (Mold.) Hensold, comb. et stat. nov. *Paepalanthus convexus* var. *major* Mold., Phytologia 15: 463. 1968. TYPE: Brazil. Amazonas: Serra Pirapucú, Rio Negro, Rio Cauaburí, Rio Maturacá, *Silva & Brazão 60926* (holotype, NY; isotypes, NY (2)).

Paepalanthus fulgidus var. *zuloagensis* Mold., Phytologia 23: 211. 1972. TYPE: Venezuela. Bolívar: Cerro de la Neblina, Planicie de Zuloaga, Río Titirico, *Steyermark 103839* (holotype, NY; isotype, NY). Syn. nov.

Paepalanthus major of Cerro de la Neblina is distinguished from *P. convexus* Mold. of Cerro Duida by its acaulescent to short-caulescent habit, its larger leaves with a smooth (not sulcate) upper epidermis, and its solitary robust inflorescences with peduncle sheaths far surpassing the leaves. Its closest allies are the sympatric *P. gleasonii* Mold., and probably *P. squamuliferus* Mold., the latter of tepui summits in the Gran Sabana.

It is distinguished (imperfectly) from *P. gleasonii* by its usually shorter stems, more sharply cuspidate leaves, and especially by the sericeous upper leaf surface, lack of well-defined cilia, and the slightly revolute margins. In *P. gleasonii*, the leaves are bluntly cuspidate, densely short-ciliate, and occasionally also hirsute adaxially at the apex, but otherwise early glabrate on both surfaces, and the margins flat in drying.

It differs from *P. squamuliferus* also by the sharply acute leaf apices, as well as by the acute to acuminate involucral bract apices. In *P. squamuliferus*, the leaves are subacute to rounded, but never sharp-cuspidate, and the involucral bracts are usually obtuse to rounded.

"*Paepalanthus fulgidus* var. *zuloagensis*," also from Neblina and known only from the type, appears to be a dwarf form of *P. major*, with smaller leaves and heads. I am provisionally placing it in synonymy pending the availability of further material.

Paepalanthus convexus, with its numerous small inflorescences, peduncle sheaths approximately equaling the leaves, and leaves strongly sulcate-ribbed on the upper surface, is a more distant relative probably derived from *Paepalanthus sulcatus* Hensold (originally described from Cerro de la Neblina as *P. stegolepoides* var. *acutalis* Mold.).

Paepalanthus parvicephalus (Mold.) Hensold, comb. et stat. nov. *Paepalanthus convexus* var. *parvicephalus* Mold., Phytologia 52: 19. 1982. TYPE: Venezuela. Amazonas: Cerro Marahuaca-Fhuif, 2,330–2,460 m, *Steyermark et al. 126100* (holotype, LL not seen).

Although both *P. parvicephalus* of Cerro Marahuaca and *P. convexus* of nearby Cerro Duida share a long-stemmed, clambering habit, they differ strongly in leaf form and inflorescence arrangement. In *P. convexus*, the leaves are acute, with the veins inscribed on the upper surface, and the whole leaf strongly reflexed at maturity, while in *P. parvicephalus*, the leaves are obtuse, the veins obscurely if at all inscribed above, and the leaves divergent, not strongly reflexed at maturity. In addition, *P. convexus* is unique for its numerous small, short-pedunculate inflorescences. Although the two taxa appear closely related, *P. sulcatus* appears on morphological and geographic grounds to be a possible common ancestor to both, even to the extent of intergrading with *P. parvicephalus* at the southern end of its range. *Paepalanthus parvicephalus* is therefore elevated to specific status in order to avoid probable misrepresentation of relationships.

Paepalanthus parvicephalus var. **wurdackii** (Mold.) Hensold, comb. nov. *Paepalanthus perplexans* var. *wurdackii* Mold., Mem. New York Bot. Gard. 8: 98. 1953. TYPE: Venezuela. Amazonas: Serranía Parú, Río Parú, Caño Asisa, 2,000 m, *Cowan & Wurdack 31141* (holotype, NY).

This taxon, native to the Serranía Parú, appears closely related to and probably derived from *P. parvicephalus* var. *parvicephalus* of Cerro Duida. It differs from this variety primarily in its smaller heads (4.5–5 mm diam. vs. 6.5–8 mm in var. *parvicephalus*). It is distinguished from *P. schomburgkii* Mold. of the Gran Sabana by the following characteristics: leaves ligulate, i.e., linear and subacute to obtuse, cuspidate, and densely long-ciliate at base, the venation not pellucid; involucral bracts of the lower series thickened and red-brown at base. *Paepalanthus schomburgkii* is characterized by broader leaves straight-tapered to an acute apex, not distinctly cuspidate, often long-ciliate, but the cilia not densely crowded at the base, and the venation pellucid. The involucres of *P. schomburgkii* are generally of a finer, herbaceous texture, and the bracts of the lower series not distinctly thickened as above.

Paepalanthus tortilis (Bong.) Koern. in C. Martius, Fl. Bras. 3(1): 354. 1863. *Eriocaulon*

tortile Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 624, t. 49. 1831. *Dupatya tortilis* (Bong.) Kuntze, Revis. Gen. Pl. 2: 746. 1891. TYPE: Brazil. Bahia: in arenosis humidis propre Ilheos, *Riedel s.n.* (LE not seen).

Paepalanthus salticola Herzog, Feddes Repert. Spec. Nov. Regni Veg. 29: 207, pl. 121, figs. i–l. 1931. SYNTYPES: Brazil. Alto Amazonas: Tiquié, Uira Poço, Uferwald, *Luetzelburg 23906* (M); Paporí, Trinidade, am Fall, *Luetzelburg 23912* (M, F photo neg. #18725). Syn. nov.

Paepalanthus tatei Mold., Brittonia 3: 158. 1939. TYPE: Venezuela. Bolívar: Auyán-tepui, 2,200 m, *Tate 1326* (holotype, NY). Syn. nov.

Paepalanthus killipii Mold., Bull. Torrey Bot. Club 68: 67. 1941. TYPE: Colombia. Santander Sur: E cordillera, Mesa de los Santos, *Killip & Smith 15299* (holotype, US not seen; isotype, F). Syn. nov.

Paepalanthus maguirei Mold., Bull. Torrey Bot. Club 75: 198. 1948. TYPE: Surinam. Tafelberg, North Ridge Cascade, Savanna I, *Maguire 24670* (holotype, NY; isotype, F). Syn. nov.

Paepalanthus tortilis owes its lengthy synonymy to wide variation in vegetative size and habit of flowering specimens. Ruhland's (1903) description of the species contains no measurements, but indicates a short or scarcely elongate stem with leaves clustered toward the apex. This is generally true of the material from eastern and Amazonian Brazil, as well as more depauperate collections from Guayana. However, much of the more recent collections from the Andes, as well as from tepui formations in Venezuela, are much more robust, often with long, uniformly leafy stems, but even in these areas, all gradations in size are found to occur, making division into discrete varieties or forms untenable. In Guayana alone, plants range from tiny rosettes with leaves 8 mm long and 1 mm wide, and peduncles of 5 cm, to clambering long-stemmed herbs with leaves 6 cm long and 8 mm wide, and peduncles up to 25 cm. According to Stützel (pers. comm.), greenhouse-grown plants in Ulm, all propagated from a single plant of Auyán-tepui, Venezuela, tended to flower in December regardless of plant age and size, resulting in flowering specimens of widely varying sizes, from 2 to 25 cm tall, and with leaf sizes varying widely as in herbarium material. Inflorescence size varies by a smaller factor, with heads ranging from 2.5–6 mm diam.

I am not entirely comfortable explaining all the variation in *P. tortilis* on the basis of age and environmental factors. For example, although large caulescent forms are known from eastern Brazil, they seem to be much rarer there and also localized. (*Paepalanthus obtusifolius* (Steudel) Koern. of Bahia is a probable example.) However, even if a genuine taxonomic distinction exists between the larger and smaller forms, the overlap in size ranges would be expected to be too great to allow identification on the basis of size alone.

Within Venezuela, plants of La Gran Sabana, regardless of size, are firmer in texture and have more rounded leaf margins than plants of Amazonas or the Andes. Specimens of particular interest are *Maguire 31718* (Serranía Guanay), a "gigas" plant with inflorescences to 8 mm diam., and *Liesner 19729* (El Pauji, Bolívar), a long-stemmed plant with large leaves, firm, ciliate involucral bracts, uniformly dark-colored flowers, and large papillate appendages. This contrasts with the fine herbaceous involucres, sepals streaked red-brown along the midvein, and filiform appendages of typical *P. tortilis*. The collection may represent a new species or a hybrid, but additional material is desirable.

Paepalanthus turbinatus (Gleason) Hensold, comb. nov. *Leiothrix turbinata* Gleason, Bull. Torrey Bot. Club 58: 331. 1931. TYPE: Venezuela. Amazonas: Cerro Duida, *Tate 775* (holotype, NY).

This species of Cerro Duida is a member of subg. *Monosperma*. It is characterized by its clumping habit, its leaves pilose on both surfaces and smooth above (the veins not inscribed), and by the floral bracts bearded abaxially with a naked long-acuminate apex.

Paepalanthus yapacanensis (Mold.) Hensold, comb. nov. *Syngonanthus yapacanensis* Mold., Mem. New York Bot. Gard. 8: 102. 1953. TYPE: Venezuela. Amazonas: Cerro Yapacana, Río Orinoco, *Maguire et al. 30782* (holotype, NY; isotypes, F, MO).

Paepalanthus yapacanensis, which does not have the medially connate petals of the pistillate flower found in *Syngonanthus*, is closely related to *P. dichotomus* Klotzsch ex Koern. and its allies, including *P. aristatus* Mold., with which it is sympatric on white sand savannas in Amazonas. It shares with these species a mat-forming, dichotomously branching habit, black wiry roots, linear obtuse leaves with silvery appressed cilia toward the apex, leathery peduncles abruptly constricted at the apex, involucral bracts with brittle hyaline margins, and a similar floral morphology. The numerous series of pale subhyaline involucral bracts suggest a superficial similarity with *Syngonanthus nitens* (Bong.) Ruhl. and *S. xeranthemoides* (Bong.)

Ruhl., which probably accounts for its original placement in that genus. Two varieties occur, both endemic to Amazonas, Venezuela, and the following is also transferred to *Paepalanthus*.

Paepalanthus yapacanensis var. **hirsutus** (Mold.) Hensold, comb. nov. *Syngonanthus yapacanensis* var. *hirsutus* Mold., Phytologia 36: 51. 1977. TYPE: Venezuela. Amazonas: 12–40 km from San Fernando de Atabapo, on road to Sta. Bárbara, *Gentry & Tillett 10869* (holotype, LL not seen; isotypes, MO, VEN).

SYNGONANTHUS

Syngonanthus acephalus Hensold, sp. nov. TYPE: Venezuela. Amazonas: Selva secundaria de San Carlos del Río Negro, 25 Jan. 1958, *Vareschi & Magdefrau 6789* (holotype, VEN; isotype, MO). Figures 3H, I, 6.

Herba perennes pulvinos formantes, habitu similis musco. Folia linearia, 1–2 mm longa, 0.2 mm lata. Flores singulatim vel binatim ad apices caulium foliosorum portati. Pedunculi et involucra carentia. Flores dimeri bisexuales actinomorphi; sepala ovata glabra; petala basin versus carnosa in medio connata; filamenta basi petalorum affixa.

Perennials forming branched mosslike mats. Roots abundant, white, spongy, slightly larger in diameter than the leaves. Stems ca. 1 cm long, fine, branched, soft-pilose. Leaves linear to ligulate, obtuse, 1–2 mm long, 0.2 mm wide, membranous to coriaceous, gently recurved-spreading, glabrous. Inflorescences reduced to 1–2 flowers, these terminal on unspecialized leafy branches and subtended by dense tufts of hair. Floral bracts present, though sometimes green and undifferentiated from foliage leaves, occasionally brownish. Peduncles undeveloped. Flowers bisexual, actinomorphic. Sepals 2, free, 1–1.3 mm long, triangular-ovate, carinate, cupped at base around locule and seed, the apex often fleshy-subterete, simulating apex of foliage leaves, cream-colored or greenish, glabrous. Petals oblanceolate to obtrullate, acute, fleshy in lower half, membranous above, the upper margins connate, with a row of stout hairs overlaying the area of fusion. Filaments adnate to petals in lower half; anthers cream, ca. 0.15 mm long. Style ca. 0.35 mm long; appendages papillose, filiform or narrowly infundibular, ca. 0.3 mm long; style branches simple, about equaling the appendages. Seeds dark red-brown, ca. 0.4 mm long, 0.3 mm wide, longitudinally striate, with fine less conspicuous transverse striations.

Additional specimens examined. VENEZUELA. AMAZONAS: sandy bana 12 km N of San Carlos, 100–120 m, 6 Feb. 1977, *Morillo & Villa 5406* (MO, VEN); on white sand 1 km E of Maroa, 125 m, 20 Apr. 1970, *Steyermark & Bunting 102837* (LL, MO, VEN).

Syngonanthus acephalus shares with *S. amazonicus* Mold. 2-merous, bracteate, bisexual flowers with the petals connate at the upper margins and fleshy below, and with the staminal filaments adnate to the corolla. However, the very reduced 1–2-flowered inflorescence of *S. acephalus*, in which peduncles and involucres are lacking, is to my knowledge not found elsewhere in the Eriocaulaceae.

This species occurs on sandy sites at low elevations in southwestern Amazonas, where it is sympatric with *S. amazonicus*.

Because of its mosslike habit, this species had previously been identified as sterile material of *Syngonanthus vareschii* Mold. (See discussion of *S. vareschii*.)

Syngonanthus duidae var. **humilis** Hensold, var. nov. TYPE: Venezuela. Bolívar. Summit of Kukenán-tepui, 2,550 m, *Liesner 23134* (holotype, MO).

Folia 0.4–0.6 cm longa. Vaginae pedunculorum 0.8–1.0 cm longae. Pedunculi 2–7 cm longi. Capitula 3–6.5 mm lata.

Perennials forming low dense colonies. Stems up to 1 cm long. Leaves linear, 0.4–0.6 cm long, the upper surface appressed-hairy to nearly glabrous. Peduncle sheaths 0.8–1.0 cm long; peduncles 2–7 cm long. Heads 3–6.5 mm diam.

Additional specimens examined. VENEZUELA. BOLÍVAR: summit of Roraima, *Delascio & Brewer 4745* (VEN); plateau below summit of Uei-tepui (Cerro del Sol), W sector, above valley of Río Arabapó, *Huber 10.030* (MO).

This variety, which is endemic to the Roraima formation in the southeastern part of the Gran Sabana, differs from var. *duidae* in its reduced leaves and peduncles. Variety *duidae*, which is widespread elsewhere in the Gran Sabana and also at high altitudes in Amazonas, typically has leaves 1–4 cm long, and peduncles up to 35 cm long.

Syngonanthus fenestratus Hensold, sp. nov. TYPE: Venezuela. Bolívar: Raudales de Canaima, 1 Oct. 1958, *Vareschi & Magdefrau 6612* (holotype, VEN). Figures 3K–J, 7.

Herba caule primario perbrevi rosulata; ramo solitario erecto parce folioso ad apicem 3–5 inflorescentias efferenti. Folia basalia linearia acuta fenestrata glandulosa

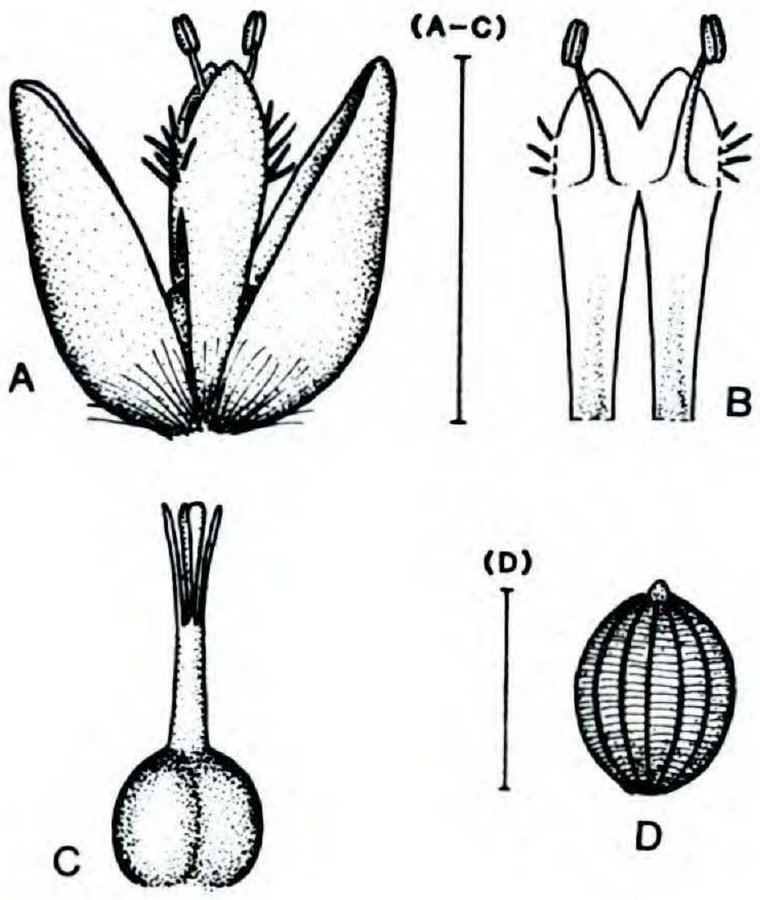

FIGURE 6. *Syngonanthus acephalus* Hensold (*Vareschi & Magdefrau 6789* VEN).—A. Flower (bisexual) with sepals spread open.—B. Corolla split open along one side.—C. Gynoecium.—D. Seed. Scale bar A–C = 1 mm; scale bar D = 0.4 mm.

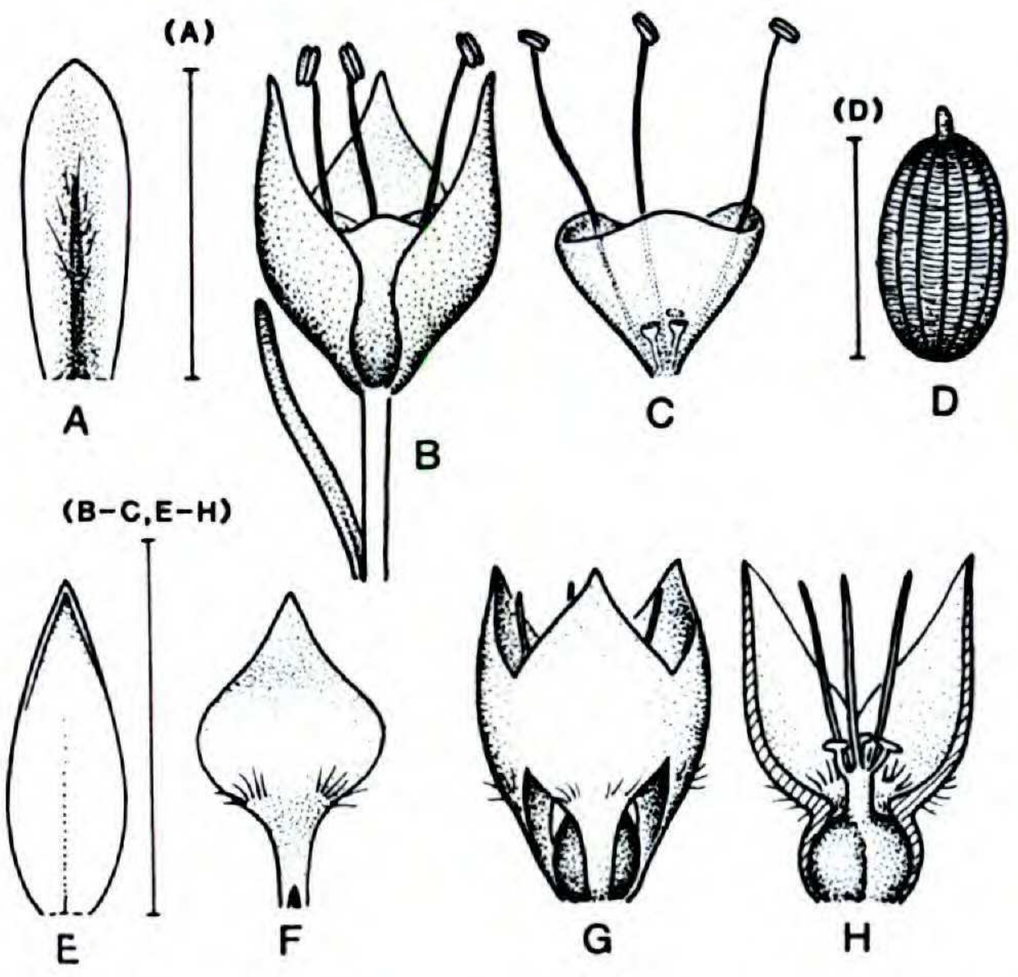

FIGURE 7. *Syngonanthus fenestratus* Hensold (*Vareschi & Magdefrau 6612* VEN).—A. Involucral bract. B, C. Staminate flower.—B. Flower with floral bract.—C. Corolla with sepals removed.—D. Seed. E–H. Pistillate flower.—E. Sepal, adaxial view.—F. Petal of flower after anthesis (margins free), adaxial view.—G. Flower at anthesis with sepals removed.—H. The same, with one petal removed, showing corolla clasping style. Scale bar A = 2 mm; scale bar B–C, E–H = 3 mm; scale bar D = 0.6 mm.

1.5–4 cm longa. Folia caulina anguste lanceolata 5–8 mm longa. Pedunculi 6-costata glandulosa. Capitula ca. 6–7 mm lata. Bracteae involucrales oblongae subhyalinae plerumque secus costam castaneae. Bracteae florales longitudine ½ florum aequantes. Flores actinomorphi; sepala elliptica acuta; corollae carnosae, lobis non-involutis, eis florum pistillatorum acuminatis.

Plants rhizomatous herbs, producing a basal rosette and a solitary erect (fertile) branch bearing an umbel of inflorescences at the apex. Roots white, spongy. Basal leaves linear, acute, 1.5–4 cm long, 0.5–0.7 mm wide, membranous, flat or subterete, fenestrate, glandular-hairy, the midvein prominently thickened. Fertile branch 3–6.5 cm long, yellow-green when young, dark reddish brown at maturity, sparingly foliose, the leaves spirally arranged, lance-linear, acute, glandular, ca. 5–8 mm long, or those clustered at apex up to 13 mm long. Inflorescences 3–5 per umbel. Peduncle sheaths 1.5–2.5 cm long, densely glandular-hairy, lax, subacute to obtuse with a narrow sinus ca. 5 mm deep; peduncles 7–13 cm long, 6-costate, glandular toward apex. Heads globose at maturity, 6–7 mm diam.; involucral bracts in ca. 2 series, oblong, obtuse, ca. 2–2.5 mm long, hyaline, reddish brown, especially along the midvein, the margins sometimes colorless, glabrous, or sometimes pilose abaxially but not along margins, becoming reflexed and lost from view upon maturation of head. Floral bracts present, linear, subacute, whitish, about half-equaling the flowers. *Staminate flowers*. Sepals 3, briefly connate at base, elliptic, acute, carinate, ca. 2.1 mm long, cream-colored, glabrous. Corolla tubular, broadly infundibular, about half the length of the sepals or less, very fleshy, the lobes nearly obsolete, noninvolute. Stamens with filaments free, strongly exsert, about equaling the sepal apices; anthers white, ca. 0.2 mm long. Pistillodes present, simulating gynoecial appendages. *Pistillate flowers*. Sepals 3, free, ca. 2.9 mm long, always cream-colored, otherwise as in staminate flowers. Petals connate at their upper margins, but separating after anthesis, broadly spatulate-acuminate, with a narrow claw at the base, ca. 2.7 mm long, very fleshy, noninvolute, with a cushionlike thickening in the middle which rests against the style, pilose on both surfaces near margins at base of fusion zone. Style very short; appendages infundibular, reddish, with a white-papillose rim; style branches simple, about equaling the petals. Seeds ellipsoidal, with a wartlike protrusion at the funicular end, ca. 0.6 mm long and 0.3 mm wide, the outer epidermis longitudinally striate, the striae swelling when wet and breaking apart to form short hairlike processes.

Additional specimens examined. GUYANA. RUPUNUNI DISTR.: Chaakoitou, near Mountain Point, just south of Kanuku Mountains, 2°56′N, 59°40′W, *Maas & Westra 4050* (MO, NY).

This species has been confused with *Syngonanthus bisumbellatus* (Steudel) Ruhl., with which it shares small stature and sparingly leafy aerial stems with spirally arranged leaves. *Syngonanthus fe-*

nestratus can be easily distinguished by its larger heads, oblong brownish involucral bracts and by the actinomorphic flowers with fleshy corollas. These floral characters, together with the fenestrate leaves, suggest alliance of the species with sect. *Carphocephalus* (Koern.) Ruhl. and perhaps especially with the widespread amphibious species *S. anomalus* (Koern.) Ruhl.

Syngonanthus humboldtii var. **parvus** (Mold.) Hensold, comb. nov. *Syngonanthus allenii* var. *parvus* Mold., Mem. New York Bot. Gard. 8: 99. 1953. TYPE: Venezuela. Amazonas: Puerto Ayacucho, *Maguire et al. 29238* (holotype, NY).

Syngonanthus humboldtii var. *parvus* is a reduced form of the widespread *S. humboldtii*, lacking verticils of leaves on the aerial stem, and limited to laja formations in the vicinity of Puerto Ayacucho, Amazonas, Venezuela. In these areas it is sympatric with var. *humboldtii*, with which it shares acute to subacute involucral bract apices, the absence of floral bracts, and acute glabrous sepal apices. This contrasts with *S. allenii* Mold. of Colombia, which is characterized by aristate involucral bracts, the presence of floral bracts, and acuminate ciliate sepal apices.

Syngonanthus macrocephalus (Mold.) Hensold, comb. et stat. nov. *Syngonanthus humboldtii* var. *macrocephalus* Mold., Mem. New York Bot. Gard. 8: 101. 1953. TYPE: Venezuela. Amazonas: Cerro Sipapo, North Mountain, 5,000–6,000 ft., *Maguire & Politi 27649* (holotype, NY).

This rare endemic of the Cerro Sipapo (northwestern Amazonas, Venezuela) is probably not closely related to *S. humboldtii* (Kunth) Ruhl., but its true affinities are difficult to interpret. Like *S. humboldtii*, its inflorescences are disposed in umbels arising from the apex of fertile aerial branches. It differs from *S. humboldtii* in that these branches are naked and usually relatively short in comparison to the peduncles, the inflorescences are few (1–5), and the heads are larger, between 5 and 10 mm diam. In addition, the peduncles are 5–6-costate, the involucral bracts are lance-acute, and the bracts and perianths of the inflorescence are suffused with coppery brown. In all of these respects, it is more similar to *S. procerus* Mold. of Central Brazil.

The type specimen is on a mixed sheet with *S. duidae* Mold., which although it lacks the stem dimorphism and involucre color of *S. macrocephalus*, bears a strong superficial resemblance to this species.

Syngonanthus minutus (Mold.) Hensold, comb. nov. *Paepalanthus minutus* Mold., Brittonia 3: 158. 1939. TYPE: Venezuela. Bolívar: Auyán-tepui, 2,200 m, *Tate 1328* (holotype, NY).

This rare species of *Syngonanthus*, endemic to Auyán-tepui and known only from the type, was originally described in *Paepalanthus* due to the lack of fusion of the petals in the pistillate flower. However, considering a wide range of characters, its closest affinities appear to lie with *Syngonanthus*, in particular *S. simplex* (Miq.) Ruhl. and *S. gracilis* (Bong.) Ruhl., both of which also occur in Venezuelan Guayana, though apparently not at altitudes higher than 1,500 m. The small size, rosulate habit, aerenchymatous roots, acicular 1-veined leaves, glabrous inflorescences, and gold subhyaline bracts and sepals of *S. minutus* immediately suggest both these species, as do particularly the falcate-asymmetric calyces of the staminate flowers. Also like these species, *S. minutus* lacks floral bracts, and has corollas in the staminate flowers raised on an androphore, stigmas undivided, and small filiform stylar appendages.

It is true that the 2-merous flowers with petals free in both sexes make the species unique as far as we know in *Syngonanthus*. However, in *S. gracilis* and *S. minutus* the posterior sepal is reduced relative to the two falcate anterior ones, and it is not difficult to imagine its complete loss in a reduction series, together with corresponding reduction in other floral parts.

The simultaneous loss of fusion in the petals of both staminate and pistillate flowers is an uncommon condition in *Paepalanthus* and *Syngonanthus*, and thus not informative with respect to generic alliance. Consistently free petals in staminate and pistillate flowers are found in *Leiothrix fluitans* (Mart.) Ruhl. and *Rondonanthus* (*Paepalanthus*) *capillaceus* (Klotzsch ex Koern.) Hensold & Giulietti, two rheophytic species whose closest relatives have petals fused in at least the staminate flowers. (See also the discussion of *Syngonanthus jenmanii* (Gleason) Giulietti & Hensold, Ann. Missouri Bot. Gard. 78: 441–464. 1991.) Free petals in staminate flowers of *Paepalanthus* subg. *Xeractis* occur sporadically as a developmental aberration (Hensold, unpublished data). Similar aberrations in *Syngonanthus* would presumably affect pistillate flower corollas as well. Thus, it may be that the loss of petal fusion in *S. minutus* is a developmental abnormality associated

with environmental stress (high altitude) or selection for the reduction of flower parts. In any event, the close apparent relationship between this species and *S. simplex* and allies, together with the presence of aerenchymatous roots and the absence of floral bracts, both characters not known to occur in *Paepalanthus*, suggests that the species is much more comfortably accommodated in *Syngonanthus* sect. *Dimorphocaulon* than in *Paepalanthus*.

Syngonanthus ottohuberi Hensold, nom. et stat. nov. *Syngonanthus similis* var. *venezuelensis* Mold., Phytologia 45: 209. 1980. TYPE: Venezuela. Amazonas: between Caño Cotúa and the W base of Cerro Yapacana, *Huber 1633* (holotype, LL not seen).

Syngonanthus densifolius var. *venezuelensis* Mold., Phytologia 48: 291. 1981. TYPE: Venezuela. Amazonas: on S bank of the Caño Yagua ca. 15 km upstream from its mouth, *Huber & Tillett 2918* (holotype, LL not seen; isotype, VEN).

Because this species was originally described as a variety with only a very short diagnosis, a full description is given here.

Plants perennials producing basal rosettes and a solitary, erect fertile branch bearing an umbel of inflorescences at its apex. Roots with a spongy white cortex and a wiry black fibrous core. Leaves of rosette linear, sharply acute to aristate, 2.2–4.5 cm long, 1–1.5 mm wide, coriaceous, striate below, smooth above, flat to revolute-canaliculate upon drying, glabrous. Fertile branch leafless except at apex, 6–12 cm long, blackish, shiny, glabrous or nearly so; involucral leaves subtending umbel lanceolate-acute, 2.5–3.0 cm long, 0.7 mm wide, striate, pubescent with spreading hairs. Inflorescences 3–10 per umbel. Peduncle sheaths 3–4 cm long, firm, pubescent with spreading hairs, the apex sharply acute with a rounded sinus. Peduncles 20–27 cm long, 3-costate, slightly ampliate at the apex, pubescent with spreading hairs and usually glabrate. Heads 7–7.5 mm diam., broadly turbinate. Involucral bracts in about 4 series, reddish gold, becoming grayish with age, subhyaline, glabrous, the outermost ovate, the inner oblong to oblong-oblanceolate, rounded, the largest ca. 2.5 mm long, enclosing but not surpassing the head. Floral bracts present, linear, nearly equaling the flowers, glabrous. *Staminate flowers.* Pedicels 0.5–0.9 mm long. Sepals 3, free, narrowly oblong-elliptic, 2.1–2.3 mm long, 0.4–0.5 mm wide, white. Corolla narrowly infundibular, about equaling the sepals, membranous, glabrous, the androphore very short. *Pistillate flowers.* Pedicel ca. 0.2 mm long. Sepals ca. 2.5 mm long, otherwise similar to those of the staminate flowers. Floral axis densely hairy between insertion of sepals and petals. Petals narrowly oblanceolate, connate from middle nearly to the apex, about equaling sepals, membranous, cream or tinged with reddish gold, glabrous. Style ca. 0.25 mm long; appendages ca. 0.5 mm long; style branches very fine, hairlike, adhering to the petals.

Additional specimens examined. VENEZUELA. AMAZONAS: Canaripó, S margin of lower Río Ventuari, 20 km E of confluence with Río Orinoco, *Huber 1905* (LL, NY, VEN); base of Cerro Yapacana, *Thomas & Rogers 2592* (NY).

Syngonanthus densifolius Silveira and *S. similis* Ruhl. are both described from the Serra do Espinhaço of Minas Gerais, Brazil, and neither is similar enough to *S. ottohuberi* to allow treatment of the latter as a variety. *Syngonanthus similis*, with a more compact habit, 2–5 aerial branches, whitish involucral bracts surpassing the disc, and floral bracts lacking, appears more closely related to *S. umbellatus* (Lam.) Ruhl. and *S. reclinatus* (Koern.) Ruhl.

I have not seen the type of *S. densifolius*, but the description indicates that it is also a more compact plant, with chartaceous, obtuse leaves and much shorter, glandular-hairy peduncles, with the inner involucral bracts lanceolate, recurved, and abaxially pilose, and the sepals also pilose.

The species is named for Otto Huber, distinguished Venezuelan botanist who collected the type, and has otherwise made extensive contributions to knowledge of the sand savannas of Venezuelan Amazonas.

Syngonanthus pakaraimensis var. **rivularis** (Mold.) Hensold, comb. et stat. nov. *Syngonanthus rivularis* Mold., Mem. New York Bot. Gard. 9: 411–412. 1957. TYPE: Venezuela. Bolívar: Chimantá Massif, C. section, headwaters of Rio Tírica, 2,120 m, *Steyermark & Wurdack 792* (holotype, NY; isotype, F).

Syngonanthus pakaraimensis Mold. is an abundant, widely varying and probably widely hybridizing species of the Gran Sabana. Although some variation exists between all populations of the tepui summits, the Chimantá population is the only one in which floral bracts are present and the involucral bracts relatively large and firm, slightly surpassing the disc, and reflexing somewhat at maturity. I have chosen to recognize it at the varietal level for the following reasons. First, the readily

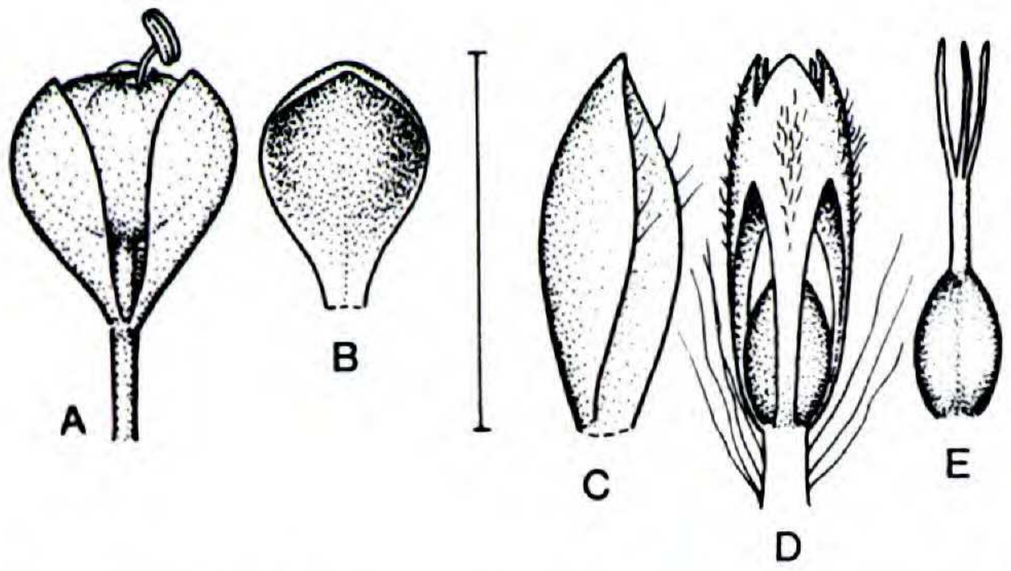

FIGURE 8. *Syngonanthus setifolius* Hensold (*Maguire & Politi 28035* NY). A, B. Staminate flower.—A. Flower.—B. Sepal, adaxial view. C–E. Pistillate flower.—C. Sepal.—D. Flower with sepals removed.—E. Gynoecium. Scale bar = 8 mm.

apparent difference between the taxa is small, especially in relation to the large amount of variation in var. *pakaraimensis* itself over its range. Second, the geographic relationship between the taxa is that considered typical of varieties. Variety *pakaraimensis* occurs on tepui summits to all sides of Chimantá but is absent from that tepui, where it is replaced by var. *rivularis*. Third, var. *rivularis* is in several respects intermediate between *S. pakaraimensis* and *S. tiricensis* Mold., another Chimantá endemic, giving reason to suspect a hybrid origin.

Syngonanthus setifolius Hensold, sp. nov. TYPE: Venezuela. Amazonas: bana on white sand, 9 km NE of San Carlos de Río Negro, 120 m, *Liesner 3857* (holotype, MO; isotype, LL). Figures 3A, B, 8.

Herba rosulata caespitosa. Folia filiformia 0.5–4 cm longa et 0.2–0.4 mm lata juventute albo-villosa. Inflorescentiae solitariae vel plures invicem sequentes. Capitula 2–2.5 mm lata. Bracteae involucrales pallidae glabrae; proximales breviter acuminatae, costis incrassatis; bracteae florales nullae. Flores staminati: sepala 3 late obovata interdum illa lateralia leviter falcata. Corollae carnosae late infundibulares lobis involutis. Flores pistillati: sepala ovato-acuminata, infra apicem ciliata. Appendices nullae.

Plants rosulate perennials. Roots spongy, white, abundant, less than 0.25 mm diam. Leaves filiform-tapered, obtuse, 0.5–4 cm long, ca. 0.2–0.4 mm wide, membranous to subterete, often recurved, the upper surface appressed-hairy or glabrate, the lower often with appressed malpighian hairs along the single prominent central vein, the entire rosette tufted with white hairs at the center. Inflorescences solitary to numerous and then produced sequentially. Peduncle sheaths green, acute at apex, coarsely pubescent with appressed hairs and sometimes also glandular-hairy. Peduncles 2.5–10 cm long, very fine, 3-costate, pubescent as the sheaths. Heads 2–2.5 mm diam. Involucral bracts white to gold, glabrous, at least the outer commonly short-acuminate with a thickened midrib, the upper oblong or obovate-rounded; floral bracts absent. *Staminate flowers*. Pedicels ca. 0.25 mm long. Sepals 3, free or sometimes irregularly fused, broadly obovate, slightly cucullate, obtuse, sometimes the two lateral slightly falcate-asymmetrical, ca. 0.5–0.6 mm long, white, glabrous. Corollas broadly infundibular and raised on an androphore, the androphore ca. 0.2 mm long, the corolla tube ca. 0.4 mm long, slightly surpassing the sepals, fleshy and bulbous, white, glabrous, involute. *Pistillate flowers*. Pedicels ca. 0.2 mm long. Sepals free, ovate, acute to acuminate, carinate, caducous, ca. 0.8 mm long, white, ciliate below the apex. Petals connate above, narrowly spatulate, about equaling the sepals, pilose abaxially below the apex. Style about equaling style branches in length; style branches simple; appendages lacking. Seeds longitudinally striate.

Additional specimens examined. VENEZUELA. AMAZONAS: Río Atabapo, *Foldats 3690* (NY); lower Ventuari SE of Carmelitas, *Huber 2685* (VEN); San Carlos, *Huber 5676* (NY); 9 km NE of San Carlos de Río Negro, *Liesner 3912* (LL, MO) and *Liesner 3914* (MO); 10 km NE of San Carlos de Río Negro, *Liesner 6925* (LL, MO), *Liesner 7034* (MO); Cerro Sipapo, *Maguire & Politi 28035* (F, NY, VEN); Río Guainía, along Pimichín–Yavita trail near Pimichín, *Maguire et al. 41793* (F, NY); between Esmeralda savanna and SE base of Cerro Duida, *Steyermark 57814* (F, NY); N of Cerro Vinilla, 30 km SSW of Ocamo, *Steyermark et al. 130347 p.p.* (F, LL); Esmeralda, *Tate 300* (NY). BRAZIL. AMAZONAS: Rio Negro, Rio Uneiuxi, 5 km above mouth, *Prance et al. 16213* (NY); Serra Aracá, 0–3 km S of Central Massif, 3 km E of Rio Jauari, *Prance et al. 28861* (MO); Serra Aracá, 1,200 m, *Prance et al. 28978 p.p.* (NY).

This minuscule species of sand savannas resembles in habit members of the difficult *Syngonanthus gracilis* complex and has been found in herbaria under various names, including *S. gracilis* var. *tenuissimus* Ruhl., *S. gracilis* var. *hirtellus* (Steudel) Ruhl., *S. densus* var. *pumilus* Mold., and *S. simplex* (Miq.) Ruhl. It differs from these species in its truly filiform leaves and its generally smaller heads. In addition, the staminate flowers are virtually actinomorphic rather than falcate-asymmetric, and the corollas are fleshy and bulbous, as is sometimes found in the perhaps related species *S. tenuis*. The thickened acuminate apices of the outer involucral bracts also are useful in identification.

Syngonanthus spongiosus Hensold, nom. et stat. nov. *Syngonanthus aquaticus* var. *caespitosus* Mold., Phytologia 24: 19. 1972. TYPE: Brazil. Amazonas: Rio Ituxi, Rio Puciari, Fortaleza Savanna, *Prance et al. 13778* (holotype, LL; isotype, MO).

Because this variety was described with only a very brief diagnosis, a full description is given here. A *nomen novum* is chosen because of prior publication of *Syngonanthus caespitosus* (Wikstr.) Ruhl.

Plants emergent aquatics, with floating leaves and stems producing erect fertile branches bearing umbels at the apex. Stems to 6 cm long, whitish, with a spongy, aerenchymatous cortex, tomentose but early glabrate, densely leafy especially at apex, and producing adventitious roots along the entire length, the roots also white and spongy. Leaves filiform, 1–3 cm long, 0.2–0.3 mm wide, subterete near base, tapered to a blunt apex, glabrous, inconspicuously fenestrate, with a single vein prominent on the lower surface. Fertile branches 1–4 cm long, solitary, naked, deep red-brown or black, sparingly arachnoid-tomentose, bearing a whorl of involucral leaves at the apex, these ca. 5–7 mm long. Inflorescences 3–25 per umbel. Peduncle sheaths 1–2 cm long, lax, obtuse at apex, glabrous or sometimes minutely ciliate around the opening. Peduncles 2.5–9.5 cm long, of differing lengths in the same cluster, 3-costate, glabrous. Capitula 3–4 mm diam. Involucral bracts in 1–2 series, oblong to oblong-obovate, obtuse, hyaline, glabrous, spadiceous, the larger ca. 1 mm long and 0.5 mm wide, well-surpassed by flowers. Receptacle densely lanuginose, the hairs protruding from between the bract bases. Floral bracts present, linear, acute, only about half-equaling the flowers or less. *Staminate flowers.* Pedicels fleshy, 0.4–0.5 mm long. Sepals 3, ca. 1.0–1.1 mm long, the lower 0.3–0.4 mm connate-tubular, the distal portions broadly ovate-elliptic, obtuse, yellowish to spadiceous, glabrous. Corolla tube borne on a fleshy obconic androphore; androphore ca. 0.4 mm long; corolla tube deeply three-lobed, infundibular, membranous, ca. 0.4 mm long, the lobes involute after anthesis. Stamens with filaments exsert; anthers white. Pistillodes present, inconspicuous, whitish. *Pistillate flowers.* Pedicels ca. 0.1 mm long. Sepals 3, free, elliptic to ovate-elliptic, acute, navicular-concave, 1.4–2.0 mm long, yellowish, glabrous or minutely ciliate. Petals linear-subspatulate, subacute, connate at the apex and tightly enclosing the styles, 1.1–1.4 mm long, glabrous. Style 0.1–0.2 mm long; appendages narrowly infundibular, ca. 0.3–0.4 mm long, papillose, the papillae white; style branches simple, ca. 0.7–0.9 mm long, about equaling the petals. Seeds longitudinally striate.

Additional specimens examined. VENEZUELA. APURE: Pedro Camejo, 9 km N of Caño Cochina de La Pica, 80 m, *Davidse & Gonzalez 15994* (LL, MO).

Although not described by its collectors as an aquatic, the stems of *Syngonanthus spongiosus* are evidently submersed or floating, buoyed by the aerenchymatous cortex. Other unusual characters of the species are the densely lanuginose receptacle and the fleshy pedicel and androphore in the staminate flower. It does not bear close affinity to any other Guayanan species.

It is also evidently not closely related to *S. aquaticus* Silveira of the Serra do Cipó, Minas Gerais, Brazil, of which it was described as a variety, in spite of sharing the aquatic habit and filiform leaves. It differs in its conspicuously elongate aerenchymatous stem, its oblong, obtuse, spadiceous involucral bracts, the presence of floral bracts, and a number of floral characters.

Syngonanthus tenuis (HBK) Ruhl., Pflanzenr. IV, 30(13): 253. 1903. *Eriocaulon tenue* HBK, Nov. Gen. Sp. I: 253. 1815. *Paepalanthus tenuis* (HBK) Kunth, Enum. Pl. 3: 282. 1855. *Dupatya tenuis* (HBK) Kuntze, Revis. Gen. Pl. 2: 746. 1891. TYPE: Venezuela. Amazonas: Yavita, banks of Río Tuamini (holotype, B not seen; F photo neg. # 10703).

Syngonanthus drouetii var. *parviceps* Mold., Phytologia 54: 68. 1983. TYPE: Venezuela. Amazonas: N edge of Maroa, *W. W. Thomas 2638* (holotype, LL not seen). Syn. nov.

Syngonanthus tenuis, with its long, white, showy bracts, might be easily mistaken for a member of sect. *Eulepis* Ruhl. Ruhland (1903) recognized on the basis of floral structure that it was more properly placed in sect. *Dimorphocaulon* Ruhl. It is probably not distant from the "*S. gracilis* complex." *Syngonanthus bulbifer*, mistakenly placed by Ruhland in sect. *Eulepis*, is here treated as an imperfectly delimited variety of *S. tenuis*.

The varieties are roughly sympatric, but only occasionally collected at the same site. Variety *tenuis* is characterized by a smaller and more delicate habit than var. *bulbifer*, and unlike var. *bulbifer* does not seem to occur south of Venezuela. Given the high frequency of hybridization in the *Syngonanthus gracilis* alliance, it seems possible

that var. *tenuis* may be the result of gene exchange between var. *bulbifer* and some smaller member of that alliance native to the Amazonian savannas.

The two varieties are keyed as follows.

1a. Leaves 1.2–5.0 cm long, 0.5–2.0 mm wide. Peduncle sheaths 1.6–3.8 cm long. Peduncles 10–27.5 cm long, ca. 1–15 per rosette. Disc of capitulum 4–5.5 mm diam., the upper bracts waxy white, oblanceolate-rounded, often held erect or slightly radiating in dry material. Flowers ca. 1.4–1.8 mm long ..... *Syngonanthus tenuis* var. *bulbifer*

1b. Leaves 0.4–3.8 cm long, 0.2–1.0 mm wide. Peduncle sheaths 0.8–2.0(–3.0) cm long. Peduncles 4–14 cm long, ca. (4–)8–60 per rosette. Disc of capitulum 2.5–4(–4.5) mm diam., the upper bracts hyaline or with waxy white streaks, obovate to broadly oblanceolate, always cupped over the disc in dry material. Flowers ca. 1(–1.4) mm long ..... *Syngonanthus tenuis* var. *tenuis*

Syngonanthus tenuis var. **bulbifer** (Huber) Hensold, comb. et stat. nov. *Paepalanthus bulbifer* Huber, Bol. Mus. Paraense Hist. Nat. 2: 499. 1898. *Syngonanthus bulbifer* (Huber) Ruhl., Pflanzenr. IV. 30: 272. 1903. TYPE: Brazil. Amapá(?): Rio Maracá, *Guedes in hb. Amaz. Mus. Paraens., no. 601* (holotype, MG not seen; isotype, B not seen, F photo neg. # 10676).

Syngonanthus drouetii Lyman B. Smith, Contrib. Gray Herb. 117: 34, pl. 2, figs. 41–43. 1937. TYPE: Brazil. Pará: 4 km S of Vigia, *Drouet 2112* (holotype, GH not seen; isotype, F). Syn. nov.

Syngonanthus vaupesanus Mold., Phytologia 2: 6. 1941. TYPE: Colombia. Vaupés: Yurupari, ca. 350 km above Mitú, *Cuatrecasas 6973* (holotype, US). Syn. nov.

Syngonanthus vareschii Mold., Acta Biol. Venez. 2(7): 50. 1957. TYPE: Venezuela. Bolívar: Auyán-tepui, Guayaraca, 1,100 m, *Vareschi & Foldats 4576* (holotype, VEN not seen; isotypes, LL, NY).

This species is based on a mixed collection. The vegetative portion included in the isotype material I have seen and also unmistakably portrayed in the original description is the moss *Octoblepharum pulvinatum* (Dozy & Molk.) Mitt. (det. Bruce Allen). The inflorescences appear to be those of depauperate material of *Syngonanthus simplex* (Miq.) Ruhl., which is common in the Gran Sabana.

Syngonanthus williamsii (Mold.) Hensold, comb. nov. *Paepalanthus williamsii* Mold., Phytologia 2: 367. 1947. TYPE: Venezuela. Amazonas: Upper Orinoco, San Antonio, *Williams 15051* (holotype, NY; isotype, F).

This species is a good *Syngonanthus*, possessing all the essential characters of that genus, i.e., petals of the pistillate flowers connate medially, trichomes of the inflorescence smooth and acute, roots white and spongy. Its habit and floral structure indicate close affinities to *S. longipes* Gleason and *S. appressus* (Koern.) Ruhl.

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